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EXHIBIT 16

E. BECK, ET AL

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Nucleotide sequence of bacteriophage fd DNA

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ABSTRACT

The sequence of the 6408 nucleotides of bacteriophage fd DNA has been determined. This allows to deduce the exact organisation of the filamentous phage genome and provides easy access to DNA segments of known structure and function.

INTRODUCTION

Small DNA viruses depend during their life cycle largely on host functions and are therefore preferred model systems for the analysis of the organisation, expression and replication of the more complex host genomes. To analyse viral genomes at the nucleotide level has become technically possible with the development of new rapid DNA sequencing techniques<sup>1, 2, 3</sup>. Complete nucleotide sequences have been reported so far for coli phage  $\phi$ X174<sup>4, 5</sup> and Simian Virus SV40<sup>6, 7</sup>. Here we report the sequence of bacteriophage fd DNA, strain 478 (Heidelberg).

Phage fd<sup>8</sup> along with f1 and M13 belongs to a group of closely related filamentous, male-specific coli phages (for reviews see ref. 9, 10). Its genome is a single-stranded circular DNA of about 6000 nucleotides which is converted to a double-stranded form in the infected cell. Eight genes have been ordered by combined genetic and biochemical analysis within the phage genome. Its detailed organisation remained, however, relatively uncertain due to the lack of protein data for most gene products. Furthermore, analysis on the nucleotide level had concentrated mainly on DNA segments with regulatory functions<sup>10, 11</sup>.

We have previously reported a preliminary nucleotide sequence of fd DNA (<sup>11</sup>, and personal communications). The aim of this publication is the rapid communication of the final sequence. A more detailed account containing the experimental evidence will be published elsewhere.

#### RESULTS AND DISCUSSION

Restriction nucleases and cleavage maps. The enzymes used, their recognition sequences and the position of cleavage sites confirmed or newly established during this work are presented in Fig. 1. All cleavage sites shown have also been identified by DNA sequencing the ends of the respective restriction fragments. With one exception, all parts of double-stranded fd can be fragmented by digestion with several of these enzymes into pieces of less than 200 base-pairs.

DNA sequencing. The chemical method of Maxam and Gilbert<sup>2</sup> was used which allowed us to read sequences up to 150 (occasionally up to 220) nucleotides. Sequences obtained were stored and processed in a computer (G. Osterburg and R. Sommer, to be published) to yield the composite sequence of 6408 nucleotides presented in Fig. 2. About 75 % of this sequence was determined from both DNA strands in fd 478. Almost all of the missing 25 % have also been sequenced in the second strand, but in the closely related phage f1. Further information was obtained for about 1000 nucleotides by RNA sequencing<sup>12</sup> and for about 600 nucleotides by the plus/minus method of Sanger and Coulson<sup>1</sup>. About 10 % of the fd sequence were also established as recognition sequences for restriction nucleases at known cleavage sites (Fig. 1 and unpublished results).

Nucleotide sequence. According to Fig. 2 fd DNA is composed of 6408 nucleotides (1578A, 2210T, 1325G, 1295C) corresponding to a molecular weight of  $2.12 \times 10^6$  daltons (sodium salt). The sequence differs from that reported earlier<sup>11</sup> mainly by an insert of 18 nucleotides in the

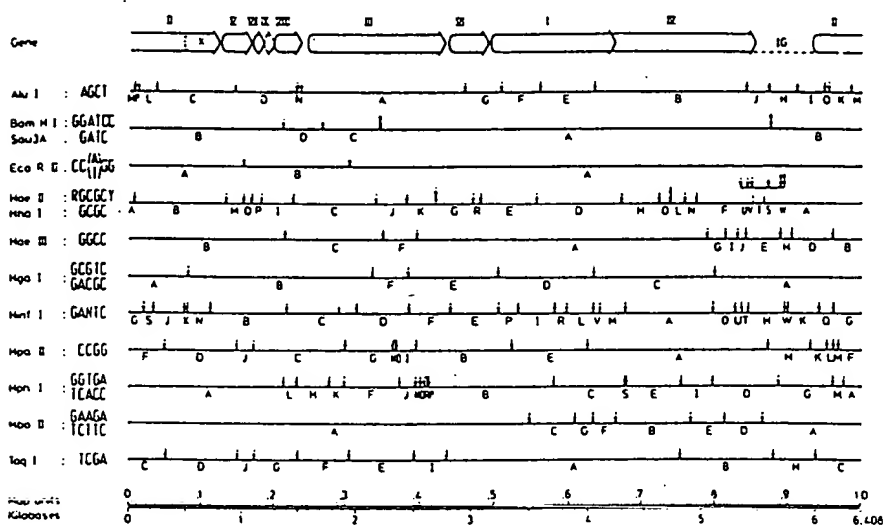


Fig. 1: Fragment maps of restriction nucleases used in the sequence analysis of fd DNA, strain 478. The known maps for HpaII, HpaI, HaeII (HinfI), HaeIII, AluI<sup>10,11</sup> were confirmed and refined. Maps for HhaI, HinfI, TaqI, BamHI, SauJA (DpnI, HbolI), EcoRII, HbolI, and HphI were newly established (E.A. Auerswald et al., M. Takanami et al., both unpublished). The first nucleotide of the recognition sites for the various restriction nucleases are listed below. An additional Hinf site has been detected in fragment HinfC (position 1858) in the DNA from fd ATCC (M. Takanami, unpublished). The circular phage DNA is opened at the unique HindII (HpaI) cleavage site. The map includes the positions and the orientation of the phage genes. IG is the intergenic space.

AluI	AGCT	39	63	229	934	1488	1517	2963	3277	3613	4097	5427	5631
		5888	6108	6135	6336								
BamHI	GGATCC	2220	5645										
SauJA	GATC	1382	1714	2221	5646								
EcoRII	CCTGG	1014	1966										
HaeII	RCGCGY	2710	4743	5560	5568								
HhaI	GCGC	44	873	1011	1085	1177	1470	2195	2467	2711	3040	3096	3599
		4313	4642	4744	4886	4996	5491	5504	5513	5535	5561	5569	
HaeIII	GGCC	1396	2245	2554	5082	5240	5346	5415	5726	5829	6181		
HpaI	GACGC	526	2164	2479	3238								
	GCGTC	4084	5159										
HinfI	GANTC	136	216	490	511	723	1403	2011	2497	2845	3259	3419	3743
		3839	4073	4118	4350	5121	5330	5376	5439	5767	5789	6043	6199
HpaII	CCGG	314	966	1095	1924	2378	2390	2396	2552	3371	4019	5615	5996
		6119	6179	6221									
HphI	GGTGA	1376	1774	1909	2398	2542	2581	2620	2626	3740	4347	4848	5118
		5707	6163										
	TCACC	1503	2635	4365	6189	6286							
HbolI	GAAGA	3913											
	TCTTC	3529	4076	4272	4938	5256	5588						
TaqI	TCGA	336	988	1127	1508	1949	2528	2815	4834	5684	6041		

repetitive sequence around position 2380. Except for a G → A transition in position 1859 the identical sequence was obtained in 2000 nucleotides from another fd strain (ATCC).

The nucleotide sequence of the related phage f1 has been determined to about 90 % (E. Beck, unpublished). It differs from the fd sequence by deletion of a single nucleotide (position 3195) and by about 160 base changes. Except for seven, these are all silent mutations which do not alter the amino acid sequence of the fd gene products.

Genome organisation. By analysing the fd DNA sequence for continuous translational reading frames - combined with the information obtained from the sequence of amber mutations in f1 and M13 (E. Beck, unpublished; J. Schoenmakers, personal communication) and from the silent base changes in f1 - allows to deduce the exact sizes and positions of the eight known gene products and of known regulatory signals. The DNA sequence predicts the amino acid sequences of known and unknown gene products, and the existence of a new gene (gene IX) in the intergenic space between genes VII and VIII<sup>11</sup>.

According to our analysis (Fig. 2) the overall organisation of the filamentous phage genome differs markedly from that of icosahedral single-stranded DNA phages, like  $\phi$ X174<sup>4</sup>: Although genes are generally closely spaced there is only one single short overlap of genes in different reading frames (at the junction of genes I and IV). In addition there is an intergenic region (IG) of 508 nucleotides which harbours the origins of DNA replication<sup>13, 14</sup>. Recent experiments show that this space can be further expanded by insertion of foreign DNA<sup>16</sup>.

Applications. fd DNA is accessible in high yields in both its single-stranded and double-stranded form<sup>10</sup>. The knowledge of its nucleotide sequence and of the map positions of a great number of restriction sites provides therefore easy access to well defined DNA molecules which can be used in different investigations on DNA structure



5787

5809 ACAACACTCA CAACIAACTC GGGCTATCTT TTTGATTAT AGGATTTTT GTCATTTCT GCTACTGCT TAAAAATAA GCTGATTAA CAATATTTA  
 5909 ACCGGAAT TAAACAACA TTAACGTTA CAATTAAAT ATTGCTTAT ACATCATCC TGTTTTGGC GCTTTCTGA TTATCAACCG GGTACATAT  
 6009 GATTGACATG CTAGTTTAC GATTACCGT CATGATCTT CTGTTTGGT CCAGACTTC AGGTAATGA CTGATAGCCT TTGTAGACCT CTCAAAAATA  
 6109 GCTACCTCT CCGCATGAA TTTATCAGCT AGAACGGTG AATATCATAT TCAGGCTGAT TGCAGTGTCT CCGGCTTTTC TCACCCGCTT GAATCTTTGC  
 6209 CTACTCATTA CTCGGCAAT GCATTAAAA TATATGAGG TTTAAANAT TTTATCCCT GCGTGAAT TANGGCTCA CCAGCAAAAG TATTACAGGG  
 6309 TCATAATGT TTTGGTACA CCGATTAGC TTATGCTCT GAGGCTTAT TCGTTAATT TCGTAACCT CTGCTGCT TGTACGATTT ATTGGATGTT  
 I  
 1 AACGCTACTA CCATTAGTAG AATGATGCC ACCTTTCAG CTGGGCCCC AATGAAAT ATAGCTAAAC AGGTTATGA CCATTGCGA AATGATCTA  
 101 ATGGTCAAC TAAATCTACT GGTCCGAGA ATTGGGATC AACTGTACA TGAATGAAA CTTCAGACA CCGTACTTTA GTTGCATATT TAAACATGT  
 201 TGAATACAG CACGAGTTC AGCAATTAG CTCTAGCCA TCCGCAAAA TCACCTCTTA TCAAAAGGAS CAATTAAAGG TACTGTCTAA TCCTGACCTG  
 301 TTGGAATTG CTTCGGTCT GGTTCGCTT GAGGCTCGAA TTGAAGCGG ATATTGAAG TCTTTCGGC TCTCTCTAA TCTTTTGTAT GCAATTGCT  
 401 TTGCTTCTGA CTATAATGA CAGGCTAAG ACCGATTTT TCAATTATGG TCAATCTCT TTTCTGAAT GTTTAAGCA TTGAGGGG ATTCANTGA  
 501 TATTATGAC GATTCCGAG TATTGGAGC TATCCAGCT AATCATTTA CAATTACCC CTCTGCCAA ACITCCTTG CAAAGCCCT TCGCTATTT  
 601 GGTTCATC GTCTCTGGT TAATGAGGT TATGATAGT TTGCTTTAC CATGCCCT AATCCTTT GCGCTTATGT AITGCAATTA GTTCAATGCTG  
 701 GTATTCTAA ATCTCAATG ATGANTCTT CCACGTGTA TAAIGTGT CCGTATGTC GTTTATTA CBTAGATTTT TCCCTCCAA GTCCTGACIG  
 801 GTATAAGAG CCACTTCTTA AATCCGCTA AGGTAATCA AATGATTAA AGTGAATAT AACCTCTC AAGCGAAT TACTACCGT TCTGTGTGTT  
 901 CTGCTCAGG CAAGCTTAT TCACTGAATG AGCAGCTTG TTACCTGAT TGGTAAAG AATATCCGT GCTGTCAAG ATTACTCTG AGGAAGTCA  
 1001 GCCAGCGTAT GGGCTGGGTC GTACACCGT GCACTGCTC TCGTCAAG TGGTAAAG AATATCCGT GCTGTCAAG ATTACTCTG AGGAAGTCA  
 1101 AAGTAAGTG GAGCAGTGG CGGATTCTA CACATTTAT CAGGCGAIGA TACAAATCT CBTGTACTT TGTTCCTCC TGGTATAAT GCTGCGGGT VII  
 1201 CAAAGATGAG TGTATTAGT TATCTTTCT GCTTTCTGT TTAGGTTGG TCGCTGTA CCGCATTA CBTATTAC CBTTTAATG AACTTCTC IX  
 1301 ATGAANAAT CTTAGTCTT CAAGCCCTC GTAGCCGTG CTACCTCTGT TCGATGCTG TCTTCCGTC CTGAGGCTGA CBTCCCGCA AAGCGGCT  
 1401 TTGACTCCCT GCAAGCCTCA GCGACCGAAT ATATCGGTA TCGGTCGGC ATGGTGGG TCAATCTCT CCGAATATC GGTATCAAGC TGTITTAAGA VIII  
 1501 ATTCACCTC AAGCAAGGT GATAACCGA TACAATTAA GGTCTCTTT GAGGCTTT TTTTGGGA TTTTCACTT CAAAAATTA TTTTCCCA  
 1601 TTGCTTAGT TGTCTCTT TATCTCAT CCGCTGAAC TGTGAAGT TGTGAAG AACTCTATC AGAAATTTA TTTACTAAG TCTGGAAGA III  
 1701 CGACAAAAT TTAGTCTGT ACGCTAATA TGAGGCTGT CTGTGGAATG CTACAGGCT TGTGTTGT ACTGGTGAGC AACTCAGT TTACGGTACA

1801 TGGGTTCCCTA TTGGGCTTCG TATCCCTGAA AATGAGGTC GTGGCTCTGA GGGTGGCGGT TCTGAGGGTG GCGGTTCTGA GGGTGGCGGT ACTAAGCTC  
 1901 CTGAGTACGG TGATACACCT ATTCCGGGCT ATACTTATAT CAACCTCTCT CAGGCACTT ATCCGCTGG TACTGAGCAA AACCCGCTA ATCCTAATCC  
 2001 TTCTCTGAG GAGTCTCAGC CTCTTANTAC TTTCATGTTT CAGATAATA GGTTCGAAA TAGGCAAGGT GCATTACTG TTTATACGG CACTGTTACT  
 2101 CANGGCACTG ACCCGTTAA ACTTATTAC CAGTACACTC CTGTATCATC AAGGCCATG TATGAGGCTT ACTGGAACGG TAAATTCCAGA GACTGGGCTT  
 2201 TCCATTCTGG CTTTAATGAG GATCCATTCTG TTTGGAATA TCAAGGCEAA TCGTCTGACC TGGCTCAACC TCTGTCAAT CTTGGCGGG GCTCTGGTGG  
 2301 TGGTCTGGT GCGGCTCTG AGGTGGCGG CTGTAGGGT GCGGTTCTG AGGTGGCGG CTTGAGGCTT GCGGTTCTG GCGGTTCTG GCGTTCGGT  
 2401 GATTCTGATT ATGAAAAAT GGCACACGCT AATAGGGG CTATGACCGA AATCCCGAT GAACACGGC TACAGTCTGA CCGTAAAGGC AACTTGGATT  
 2501 GTGCGCTAC TGATTACGGT CTTGCTATCG ATGCTTTCAT TGGTACGCTT TCGGCTCTG CTANTGGTAA TGTGCTACT GGTGATTTTG CTGGCTCTAA  
 2601 TTCCCAATG GCTCAAGTGG GTGACGGTGA TATTACCT TTAATGATA ATTTCCGTCA ATATTACCT TCTTGGCTC AGTCGGTGA ATGTCGCCCT  
 2701 TATGCTTTG GCGCTGGTAA ACCATATGAA TTTCTATTG ATTGTGACAA AATAACCTTA TCCGTTGGG ICITTCGGT TCTTTATAT GTTCCACCT  
 2801 TTAAGTATG AITTCGAGC ITTCGTAACA TACTGGTAA TACGAGTCT TAACTGCC AGTTCITTTT GGTATTCCT TATTATTCG TTTCTCTGGT  
 2901 TTCTCTCTGG TAACCTTGT CCGCTATCTG CTATCTTC TTAAGAGG CTTCGTAAAG ATAGCTATTG CTATTCATT GTTCTTGGT CTATTTATG  
 3001 GCGTTAATC AATTCTCTG GGTATCTCT CTGATATTAG GGCACATTA CCGTCTGATT TTGTTACGG CATTACAGTTA ATTCGCCGT CTAATCGGT  
 3101 TCCGCTTCTG TATGTTATC TCTGTAAA GGTGCTATT TCAATTTTG AGGTAAACA AAAAACTGTT TCTATTTGG ATTGGATAA AAAAAATGG  
 3201 CCGTTATTT TGTACTGGC AATTAGGCT CTGGAAGAC GCTGTTAGC GTTGGTAAAG TTACAGATAA AATTGAGCT GGGTGCAMAA TAGCACTAA  
 3301 TCTTGATTA AGGCTTCAAA ACCTCCGCA AGTCGGAGG TTGCTAANA CCGCTCGGT TCTAGATA CCGGATAAGC CTTCATTTT TGAATTCCT  
 3401 GCTATTGGTC GTGGTAAATG TTCTACGAC GAATATAAA ACGTTTGTCT TGTCTTGTAT GAATCGGTA CTGGTTAA TACCGTTCA TGAATGACA  
 3501 AGGAACACA GCGGATTATT GATGCTTCTG TCAATGGGA TGGATATTA TTTTCTGT TCAAGATTA TCTATTGTTG ATAAACAGC  
 3601 GCGTCTGCA TTAGTGAAC ACGTTGTTA TTGTCGGCT CCGACAGAA TTACTTTACC CTTTGCGGC ACTTTATAT CTCTGTTAC TGGCTCAAAA  
 3701 ATGCCCTGC CTAATATCA TGTGGTGT GTTAATATG GTGATCTCA ATTAGCCCT ACTGTCAGC GTTGGCTTA TACTGGTAAG AATTATATA  
 3801 ACCGATATGA CACTAAACAG GCTTTTCCA GTAAATATGA TTCAAGTGT TATCATATT TACCCCTTA TTTATCAC GGTGCGTATT TCAACCAT  
 3901 AATTATAGT CAGAGATGA AATTAACTAA AATATATTTG AAAAACTT CTGCGTCTCT TTGCTCTGG ATAGGATTTG CATCAGCAT TACATATAGT

4001 TATATAACCC AACCTAACCC GAGGTAAAG AGGTAGTCT CTCAGACCTA TGATTGTAG AAATTCACCTA TTGACTCTTC TCAGCGTCTT AATCTAAGCT  
 4101 ATCGCTATGT TTTCAAGGAT TTAAGCGAA AATTAAITAA TAGCAGCAT ITACAGAGCC AGGTTATTC CATACATAT ATTGAITTAI GTACIGTTC  
 4201 AATTAAAAA GGTAAITCAA ATGAATITGT TAAATGTAAT TAATTITGT TCTTCATGT TGTTCATC ATCTCTTT GCTCAAGTAA TTGAATGAA  
 4301 TAAITGCCCT CTGGCGGATT TCGTGACTTG GTATTCANAG CAACAGGTG AATCTGTTAT TGCTCAGCT GATGTTAAAG GTACAGTGAC TGTATATCC  
 4401 TCTGAGGTTA AGCCTGAAA TTAAGCAAT TTTCTTATCT CTGTTTACG TCGTAAAT TTTGATATCG TTGGCTCAAT TCGTCCATA ATTCAAGAT  
 4501 ATACCCCAA TAGTCAGGAT TATATTGATG AATTCGCATC ATCTGATATT CAGCAATATG ATGATAATTC CGTCTCTCT GGTGTTCT TGTTCGGA  
 4601 AATGATAAT GTTACTCAA CATTTAAAT TAAATAGCT CCGCAAGG ATTTAATAG GGTGTAGAA TTGTTGTTA AATCTAATAC ATCTAATCC  
 4701 TCAATGTAT TATCTGTGA TGGTTCAAC TTATTAGTAG TTAGCGCCC TAAAGATATT TTAGATACC TTCCCAAT TCTTCTACT GTTGATTTC  
 4801 CAACTGACCA GATATGATT GAAGGATTA TTTTCAGGT TCAGCAAGGT GATGCTTAG ATTTTCTT TCTGCTGCG TCTCAGCGCG GCACTGTCC  
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 5101 TTAAGCTCG TGTAACTGCT GAATCTGCA ATGTAAATTA TCCATTTCAG ACGTTGAGC GTCAAAATGT TGGTATTCT ATGAGTGTT TCCCGTTGC  
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 5301 GCGACAACG TTAATTCGG TATGCTGCA ACTCTTTTGC TCGGTGCTCT CACTGATTAC AAAACACTT CTCAGATT TACTAATCA AAGAAGTAT  
 5401 AATACCTTT AATCGGCTC CTGTTAGCT CCGTTCTGTA TTTCAAGAG CAAGACAGT GTACGTGT GGTCAAGCA ACCATAGTAC GCGGCTGA  
 5501 GCGGCGCAT AAGCGCGCG GGTGTGCTG TACGCGGAG COTGACCGT ACTTTGCCA GCGGCTCT TCGGCTCT TCGGCTCT TCGGCTCT  
 5601 TCTGCCACG TTTCTCGCT TCCCGCTCA AGCTTAAT CCGGGATCC CTTAGGGT CCGATTAGT GCTTTACGG ACCTCGACT CCAAAACTT  
 5701 GATTGGGTG ATGTTTACG TAGTGCGCA TCGCCTGAT AGACGGT TCGCCTTTC ACGTTGAGT CACGTTCTT T

Fig. 2: Nucleotide sequence of bacteriophage fd. The viral DNA single-strand is shown in 5' to 3' polarity. The circular DNA has been opened at the position of the origin of viral replication<sup>13,14</sup>. Numbering of nucleotides starts at the unique HindII (HpaI) cleavage site. Genes are boxed, recognition sites for the restriction nucleases shown in Fig. 1 are overlined. The sequence is available on request on magnetic tape.

and function. For example they have been used as size markers in their intact or restricted form, for the search for recognition sequences of restriction nucleases<sup>17</sup>, in the site-specific modification of the fd genome for use as a cloning vehicle<sup>16</sup>, for the isolation and the cloning of regulatory signals from fd DNA, for the analysis of integration and loss of transposon Tn-5 (<sup>16,14</sup>, E.A. Auerswald, to be published), and for the correlation of thermal denaturation profiles of DNA molecules with their nucleotide sequence<sup>18</sup>.

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